

The entire book is on heavy coated paper. With all the information it contains, with all the color photographs, and with its inexpensive price, this book is definitely a bargain. Shull and the Indiana Academy of Sciences are to be congratulated on a job well done.—*Frederick H. Rindge, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.*

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**Taxonomy, Phylogeny, and Biogeography of *Asterocampa* Röber 1916 (Lepidoptera, Nymphalidae, Apaturinae).**—Tim Friedlander. *Journal of Research on the Lepidoptera*, 31 Dec. 1987 25(4):215–338, 13 figures, 11 tables, 22 plates. Available % Santa Barbara Museum of Natural History, 2559 Puesta Del Sol Road, Santa Barbara, California 93105.

This is an important work for lepidopterists, systematists and biogeographers because of the variety of data sources and methods used to determine results. Friedlander's study comprises an entire issue of the *Journal of Research on the Lepidoptera* in monographic format.

Friedlander's work, refined from his 1985 doctoral dissertation at Texas A&M University, is essentially a completion of research originally initiated by the late Dr. Walfried J. Reinthal of Tennessee. Reinthal studied *Asterocampa* ("Hackberry Butterflies") for many years, hand-pairing, rearing and cross-pairing many of the Nearctic taxa. As Friedlander notes, results of Reinthal's work (communicated mostly through correspondence) were widely cited by lepidopterists in systematic and faunal studies. The meticulously catalogued Reinthal collection (willed to the Carnegie Museum of Natural History) served as a major reference in Friedlander's research. The time elapsed in the Reinthal and Friedlander studies can be illustrated by my mentioning that twenty-four years ago I sent live ova to Reinthal for rearing and cross-pairing of the western Great Plains *Asterocampa*!

Rarely in works concerning Lepidoptera (or entomology in general) is cladistic methodology applied to data including (i) morphology of adults and immature stages, (ii) life histories and foodplant relations, (iii) behavior, (iv) cross-pairing/rearing experiments and (v) biogeographic data. Revisionary works normally utilize some of these data; then workers debate what alternative results might have been possible with more data. Consequently, in recent years, no other issue has divided lepidopterists more than morphological versus biological species definitions and how to apply the obligatory categories of the Code of the International Commission on Zoological Nomenclature. Thus, as an example of how such various data sources affect a cladistically-based revisionary study, the *Asterocampa* monograph is a seminal work. Friedlander is aware of this, amply addressing how various data bases, and methodological views, might affect the study. There is no particular prejudice in how he proceeds.

The monograph treats a relatively small monophyletic group. Four species are recognized, with a distribution including the Nearctic plus Mexico and the Antilles. For butterflies, the group is particularly non-vagile. *Asterocampa* are well documented "perching" (versus "patrolling") species, with adults notably restricted to foodplant

micro-habitats. With such a small group, available data per taxon for the Nearctic species is about even. Unfortunately, the exception to this balance—lack of comparable data for evaluating reproductive isolation in the Antillean and Mexican *Asterocampa*—leaves unresolved a major question concerning the taxonomy and evolution of this group.

Taxonomic sections are compact, with keys provided for adults, larvae, pupae and eggs. Synonymies and general literature citations are rather abbreviated (the author frequently referring the reader to materials in the 1985 dissertation). Discussion of materials and methods is detailed, with sections summarizing morphological, biological and behavioral data along with cross-pairing/rearing experiments. Synthesis of results appears in two sections, "Phylogeny" and "Biogeography." In the phylogenetic analysis, the PAUP computer package and Wagner Tree method are applied to a 20-Character by Outgroup + 10-Taxa data matrix and their results compared. Characters include egg, larvae, pupae and adult morphology (including wings and genitalia), host plant data, behavior and geographic distributions. The outgroup consists of other taxa of the Apaturinae, *Asterocampa* being considered the sister group of Old World *Chitoria*, *Dilipa*, *Euapatura*, and possibly *Thaleropis*.

A Wagner Tree from these data indicates four terminal groups and is congruent with the four terminal branches of a diagram produced by PAUP for the outgroup plus ten subspecific taxa. Friedlander determines the presence of four "species" based on the congruence of the four taxon statements and what is experimentally known concerning reproductive isolation. He acknowledges that, cladistically, reproductive compatability is a symplesiomorphy; thus, he considers experimentally-documented reproductive isolation a possible synapomorphy. This approach is new in lepidopterology and may set a precedent for studies which contain experimental data on reproductive isolation. As Friedlander notes, previous treatments of *Asterocampa* based on wing pattern and morphology had included upwards to twelve species.

Friedlander recognizes two major clades within *Asterocampa*: (i) the "Celtis Group" (polytypic Nearctic *A. celtis* and relatively homogeneous Mexican/SW United States *A. leilia*), and (ii) the "Clyton Group" (relatively homogenous Nearctic *A. clyton* and polytypic Mexican/Antillean *A. idyja*). The "Celtis Group" is assessed as having the most advanced characters with the "Clyton Group" considered relatively plesiotypic. In comment, Friedlander notes he is including within *A. idyja* phenotypically dissimilar Mexican and Antillean populations, the former being notably mimetic but not the latter. He remarks that character differentiation was perhaps poorest for the *A. idyja* complex and that no cross-pairing/rearing experiments were possible with these taxa.

The phylogenetic results lead to great interest in the author's assessment of biogeography. Friedlander's choice of *Chitoria* dispersal across a Bering Land Bridge as the origin of Nearctic *Asterocampa* is slightly disappointing. From reading his literature review, one cannot help think he really meant vicariance of ancestral *Chitoria*/*Asterocampa* populations already in place (especially since another endemic New World apaturine assemblage, *Doxocopa*, is acknowledged as having evolved in such a fashion).

Concerning speciation within *Asterocampa*, Friedlander argues convincingly that vicariance of the geographically sympatric "Celtis" and "Clyton" groups resulted not

from macro-geographic separation but by divergence of oviposition and host plant strategies. Restricted to respective "new-growth" and "old-growth" oviposition and feeding habits, members of the two groups segregate into distinctive micro-habitats. With similar clarity, Friedlander attributes speciation within the "Celtis Group" to the xeric (southwestern U.S./Mexican) adaptation of *A. leilia* coupled with a series of Pleistocene isolation events forming components of polytypic *A. celtis*.

Clarity concerning Antillean/Mexican allopatry is, however, more problematic. Here, Friedlander has an understandable lack of good data and many presuppositions of current lepidopterology working against him. He is stuck with his subspecies clustering of Antillean nominate *A. idyja* and Mexican *A. idyja argus*, but also with the reality of *Asterocampa* being apparently poor dispersers. Here, in an otherwise elaborate study, it is truly unfortunate that character and cross-pairing/rearing data were not available for the Neotropical taxa. Based on the sister group status of these populations from the Wagner and PAUP data, Friedlander can only extrapolate possible reproductive potential from its occurrence in the Nearctic *A. clyton* complex. Thus, his speculation that *A. idyja* and *A. argus* are conspecific will be controversial. Because of these circumstances, Friedlander chooses a compromise vicariance/dispersal explanation for the origin of Antillean *Asterocampa*—since the Antilles are too old for the speculated age of *Asterocampa*, over-water dispersal to the Antilles must have taken place at a time when tectonic actions had moved the Antilles only a minimal distance from the mainland.

Future cladistic data on Caribbean butterflies may alter this common view that the Greater Antilles are too old for tectonic vicariance to have caused speciation in their butterfly faunas. By rigorous character analysis, the most recently discovered fossil Nymphalidae, from the Oligocene, appear to be congeneric with modern taxa (L. D. and J. Y. Miller, 1988 presentation to 39th Annual Meeting of the Lepidopterists' Society). This pushes back even farther lepidopterists' views of how ancient certain contemporaneous lineages may be. With the Friedlander monograph, published cladograms are available for three groups of mainland/Antillean butterflies: *Asterocampa*, *Anetia* (Danaiidae) (P. R. Ackery and R. I. Vane Wright, 1987, Milkweed Butterflies, Their Cladistics and Biology. British Museum (Natural History) / Cornell Univ. Press, vii + 425 p.) and *Nesiostrymon*/ *Terra* (Lycaenidae) (K. Johnson and D. Matusik, 1988, Ann. Carnegie Mus. 57:221–254). All three groups have terminal assemblages with mainland/Antillean bifurcations, and each contains notably micro-habitat restricted or non-vagile butterflies. A cladogram for the extremely vagile Neotropical "Prepona" butterflies (Nymphalidae) (ms. in prep. by me and Henri Descimon (Universit  de Provence, France) indicates that only members of its relatively primitive stem (*Archaeoprepona*) occur in the Antilles. The latter is somewhat surprising, considering the species richness of the more structurally advanced sister genus *Prepona*. If over-water dispersal was a common phenomenon among butterflies, it would seem as likely that *Prepona* would also have Antillean representatives. Thus, one comes away from Friedlander's *Asterocampa* scenario aware of his predicament, but somewhat unsatisfied.

Obviously the "jury is only beginning to come in" concerning cladistics, vicariance, dispersal and Antillean butterflies. However, cladograms to date do not provide obvious examples of dispersal and contain, at least, strong hints at geographic vicariance. Friedlander's data on New World *Asterocampa* are one piece in this puzzle



and his monograph gives a rich background upon which someone can attack the apparently open issue of Antillean biogeography and Hackberry Butterflies.—*Kurt Johnson, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.*

### Behavior

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**Evolutionary Genetics of Invertebrate Behavior.**—M. D. Huettel (ed.). 1986. Plenum Press, New York, ix + 335 pp. \$59.50.

Mayr (1963) has argued that evolutionary transitions to new niches or adaptive zones are generally initiated by changes in behavior. Given this and the bewildering diversity of invertebrates, both in terms of species numbers and ecological niches occupied, studies of the genetics of their behavior should contribute substantially to our understanding of the biological world. The present volume brings attention to the potential importance of such studies and, I hope, will serve to attract more students into this field. It comprises 30 chapters contributed by well-known figures in the fields of behavioral genetics and evolutionary ecology. The general areas covered include: (1) genetic variation in natural populations for courtship and mating, oviposition behavior, non-reproductive interactions among conspecifics, and life history traits; (2) molecular and biochemical genetics of behavior; and (3) some theoretical considerations of the role of behavior on evolution and speciation. Thus, a lot of important ground is covered.

Unfortunately, this volume has some serious shortcomings. First, it is quite narrowly focused with respect to the organisms and topics covered. All of the empirical chapters except one, which considers egg laying behavior in *Aplysia*, are concerned with insects and spiders, and 10 of these deal with *Drosophila*. A number of important topics, such as dispersal polymorphisms, insect social behavior, kin recognition, and general habitat selection, are not covered.

A second problem is that the book was out of date by the time it was published. This volume is the outcome of a meeting that was held in March of 1983, yet the proceedings were not published until 1986. Only three of the chapters included references to papers that appeared after 1984, and one refers to a paper that actually came out in 1983 as “in press.”

Other oddities include chapters that do not deal with or mention behavior, such as that by Scriber et al. on color polymorphism in tiger swallowtails and that by Slatkin and Kirkpatrick on the general use of quantitative genetics for evolutionary studies, and a reference by Carde to “Teal et al. (this volume),” a non-existent chapter.

Finally, the quality of the science in many studies of the evolutionary genetics of behavior, including some in this volume, leaves something to be desired. The most serious problems are lack of true replication of experiments, and making genetic interpretations based on small sample sizes without taking into consideration the power of statistical tests used. For instance, suppose one crosses two interfertile species and then backcrosses the hybrids to one of the parents. If, in the backcross